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THE ECOLOGICAL LIFE HISTORY OF CERTAIN SPECIES OF RIBES AND ITS APPLICATION TO THE CONTROL OF THE WHITE PINE BLISTER RUST

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This study is a portion of the outcome of one season's field work upon the ecology of the gooseberries and currants in New England and the Adirondacks, undertaken for the White Pine Blister Rust Control Office of the Bureau of Plant Industry, and published here with the permission of that organization. Since *Ribes* is recognized as the most critical point in the attempt to control the disease, a thorough investigation of the life history of the various species was determined upon; the present summer's work constitutes merely a beginning. In its prosecution a number of points developed, of scientific as well as practical importance, which seem of sufficient value to warrant publication. Aside from its intrinsic results, the work is of interest in that it indicates the close relationship that is likely to be found between plant and animal factors in the investigation of an ecological problem. It also embodies the promise of a useful field and large opportunity for a new profession, that of the "consulting ecologist".

Such a study will yield far greater results if attacked from the developmental standpoint; in fact, the conclusions here presented could hardly have been attained without the prerequisite of an adequate knowledge of the successional relations of the vegetation. The logical method of presentation is therefore to begin with an outline of those communities and successions of the region which are pertinent, and to follow this with a discussion of the rôle of *Ribes* therein. Finally, the principal applications of practical value in combating the disease will be suggested.

I. Climaxes and Successional Development

The area comprising New England and the Adirondacks is dominated by two forest climaxes. The Northeastern Conifer Climax, in which red spruce, *Picea rubra,* white spruce, *Picca canadensis,* and balsam fir, *Abies balsamea,* are the principal species, probably controls the northern part of Maine, and certainly the upper altitudes of the higher mountains. The Eastern Deciduous Climax dominates the remainder. This must be subdivided into a northern and a southern phase. In the former, sugar maple, *Acer saccharum,* beech, *Fagus grandifolia,* and hemlock, *Tsuga canadensis,* are the character trees, and yellow birch, *Betula lutea,* and sweet birch, *Betula lenta,* are frequently of importance. The region controlled by this type includes southern Maine, most of New Hampshire and Vermont excluding the higher mountains, the Berkshires in Massachusetts, and the northwestern corner of Connecticut. Characterizing the latter phase, which controls southern New England, we find in addition to the above trees, which here hold a relatively minor place, a number of species of more southern range, including chestnut, *Castanea dentata,* and several oaks and hickories. Between the two climaxes, and the two divisions of the more southern one, there are naturally wide belts of transitional character.

The two phases of the deciduous forest differ strikingly in relative abundance of *Ribes,* the northern being characterized by a larger number of species and of individuals, the southern by paucity of both. White pine, *Pinus strobus,* also, toward the saving of which the present study is a contribution, finds its principal home within the area controlled by the northern phase of the deciduous forest, and plays a successional rôle leading toward the ultimate establishment of that type. This constant and close companionship between the two host plants of the blister rust plainly indicates the field of our discussion. One is justified, however, in applying the main conclusions as to the life history of *Ribes* to the southern phase as well, and for considerable distances southward and westward.

The primary successions[1] of the region must be passed over, since their importance to our problem is slight. The secondary successions,[1] on the other hand, are extremely important, and a rather detailed analysis is essential.

It should be stated at the beginning that the virgin deciduous climax which once formed a magnificent forest cover has been almost totally destroyed since the advent of the European invaders. Only here and there, and largely in the depths of the mountains, may one find areas that can safely be accepted as primeval. The period of settlement, however, has been sufficiently long to permit the attainment in many places of a close approximation to the original conditions through redevelopment. The whole area is a hodgepodge of successional communities, representing all stages from pioneer to climax.

The initiating cause of secondary development is the total or partial removal of the forest through fire, lumbering, or clearing for agricultural use, followed by abandonment. A combination of the last two is very important. The timber is removed, and crops or orchards are planted, or the ground is devoted to pasturage. Widespread abandonment of such areas has taken place during the last century, and has been followed immediately by the initiation of secondary succession. It is hardly possible to differentiate separate lines of development. There is infinite variation depending on such factors as degree of thoroughness of forest destruction, degree of modification of habitat by culture, proximity of seed sources of various species, subsequent disturbances. In brief and very general outline the process is as follows.

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[1] Clements, F. E., "Plant Succession," p. 60, Carnegie Inst. of Washington, D. C., 1916.

The first stage is made up of various weeds and grasses. It is quickly superseded unless the area is pastured, in which case a solid turf is ordinarily formed which may maintain itself for a long period.

The second stage comprises a number of shrubby species, which are so characteristic that they may be aptly designated "pasture shrubs." In approximate order of importance these are wild red raspberry, *Rubus idaeus aculeatissimus,* hardhack, *Spiraea tomentosa,* meadow sweet, *Spiraea latifolia,* blueberry, *Vaccinium pennsylvanicum,* juniper, *Juniperus communis,* moun-

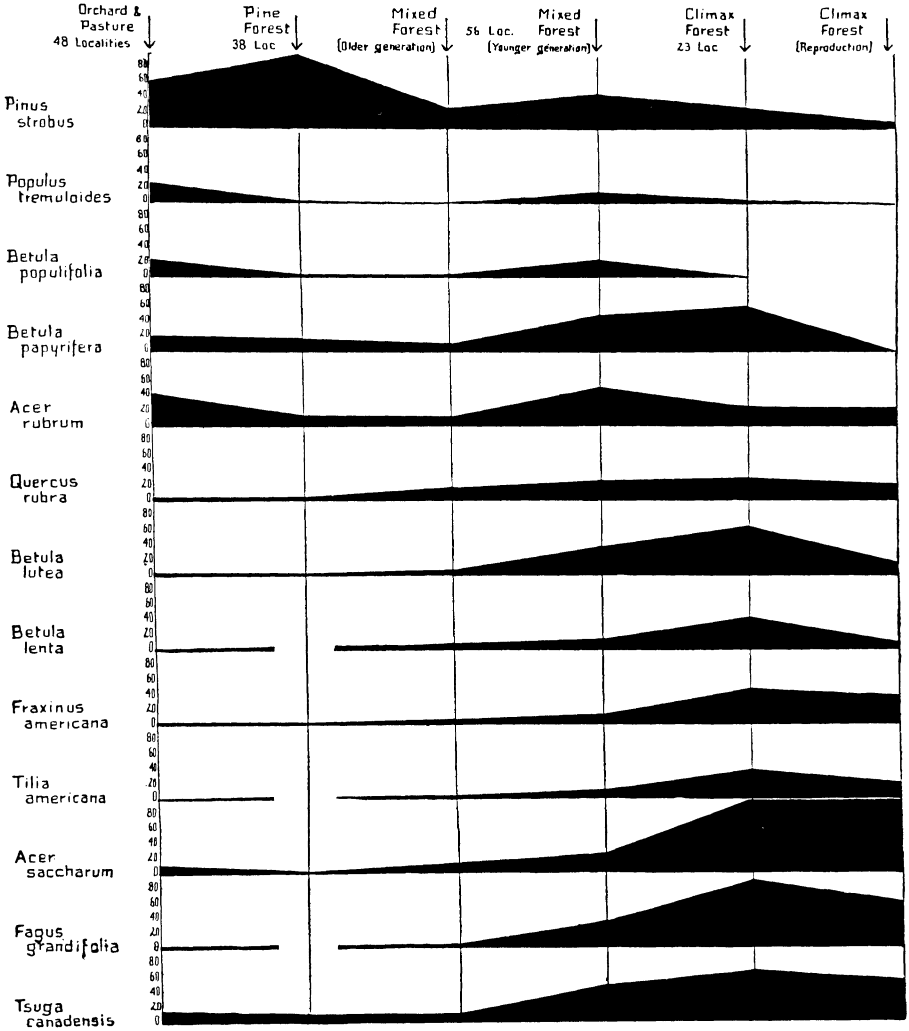

FIG. 1. Successional rôles of thirteen important trees.

tain blackberry, *Rubus allegheniensis,* high bush blueberry, *Vaccinium corymbosum,* staghorn sumac, *Rhus typhina,* and shrubby cinquefoil, *Potentilla fruticosa.*

Of rather minor importance to the successful development as a whole, but all-important to the present subject, are three species of *Ribes: R. cynosbati, R. hirtellum,* and *R. rotundifolium,* the first universally abundant, the last two of consequence within their respective ranges.

The pasture shrubs are superseded in turn by a community embracing a number of tree species, mostly semi-xerophytic, which appear here and there among the shrubs and gradually give rise to open woodland and later to closed forest. The five most important species are white pine, aspen, *Populus tremuloides,* grey birch, *Betula populifolia,* white birch, *B. alba papyrifera,* and red maple, *Acer rubrum.* These may occur in any combination, so that a multitude of indefinable communities results. Very frequently, because of proximity of seed trees, white pine forms a practically pure stand. The seedling growth under these trees is a prophecy of the final stage. Sugar maple, beech, and hemlock are the most important species, and yellow birch, sweet birch, red oak, *Quercus rubra,* white ash, *Fraxinus americana,* and linden,

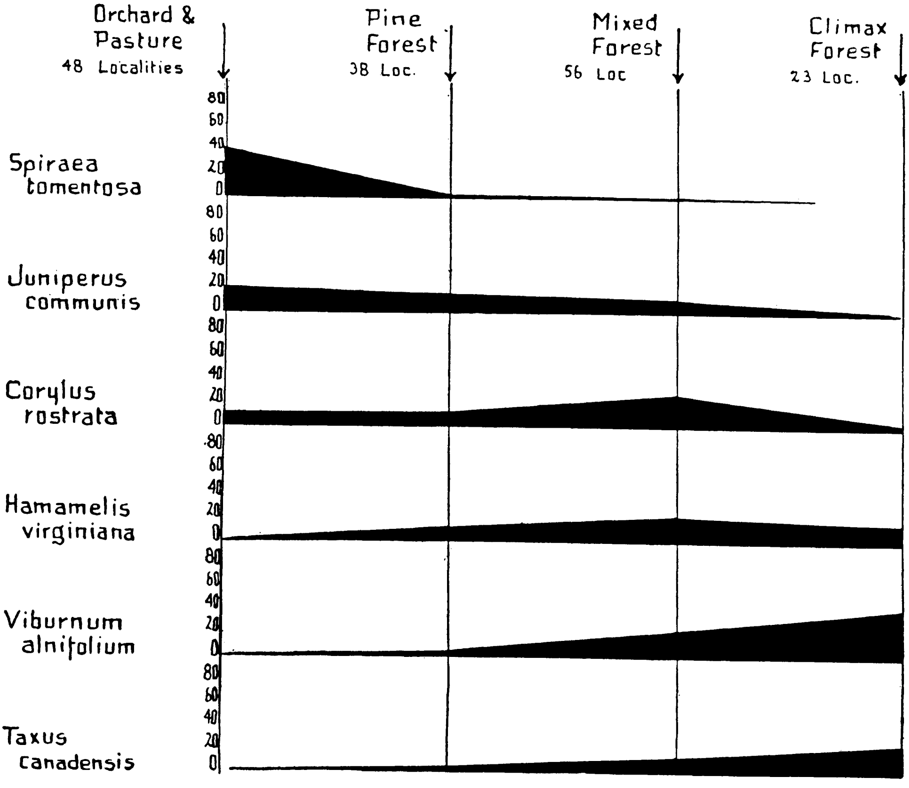

FIG. 2. Successional rôles of six important shrubs.

Tilia americana, are common. The maturing of these brings back the climax, and a study of the seedling growth in areas of adult climax forest confirms the permanence of the type, with the first three species continually increasing their dominance.

Since the habitat conditions in the region are rather uniformly mesophytic, it is not surprising to find these four stages more or less telescoped, the trees beginning to come in with the pioneers, but not attaining to dominance until later.

An attempt has been made in figures 1 and 2 to represent graphically the course of the secondary succession. In figure 1 the successional rôles of thirteen important trees are shown by indicating the percentage of the total number of localities of each stage in which the species was found to be present. The method is necessarily imperfect, since it expresses merely occurrence and gives no indication of relative abundance. The open pioneer stages have been grouped under the heading "orchard-pasture". The pine forest stage is an alternative which may be omitted, as the course of development frequently passes directly into the "mixed forest" community, which includes the large number of penultimate groupings which defy logical analysis. The climax character of sugar maple, beech, and hemlock is very evident. The reproduction beneath the trees of the climax has been added to suggest the future history. Figure 2 indicates in the same manner the successional rôles of six important shrubs: two pioneer, two intermediate, and two climax.

II. THE RÔLE OF RIBES IN SUCCESSIONAL DEVELOPMENT

a. Occurrence in Various Stages of the Secondary Succession.—The species of importance are mainly the gooseberries: *Ribes cynosbati, R. hirtellum, and R. rotundifolium.* These undoubtedly differ in preferred habitat, but not to an important degree, and my data are not sufficient to warrant separate treatment. Figure 3, in which records of the three species are combined, shows that the gooseberries occur most commonly in the orchard and pasture communities, and that they here bear most fruit and are most generally infected; that they are less common, with less fruit and infection in the mixed woodland; and least in number and infection in the climax forest. Here again we have records of occurrence only, with no indication of abundance. The descriptive field notes, however, supplement the statistical data in a very satisfactory way. They show that the plants of the pastures and orchards are almost always large, bushy, heavily fruiting, heavily infected, and that those of the mixed woodland are slender, weak, with little fruit, and moderately infected. The figures for the climax forest need some special words of explanation. The list includes a few localities that are undoubtedly primeval, together with a much larger number showing approximation to original condition through redevelopment. The eight occurrences of *Ribes* in the climax forest are unimportant, and almost entirely in openings of various kinds. The two occurrences of fruit are noted thus: "one *Ribes lacustre* beside main stream, fruiting abundantly"; "one berry". The two cases of infection were slight. Thus, if relative importance of record could be expressed in the figure, the rise of the curve of fruiting to the climax would be eliminated and the downward trend of the infection curve intensified, thus bringing the results into full consistency.

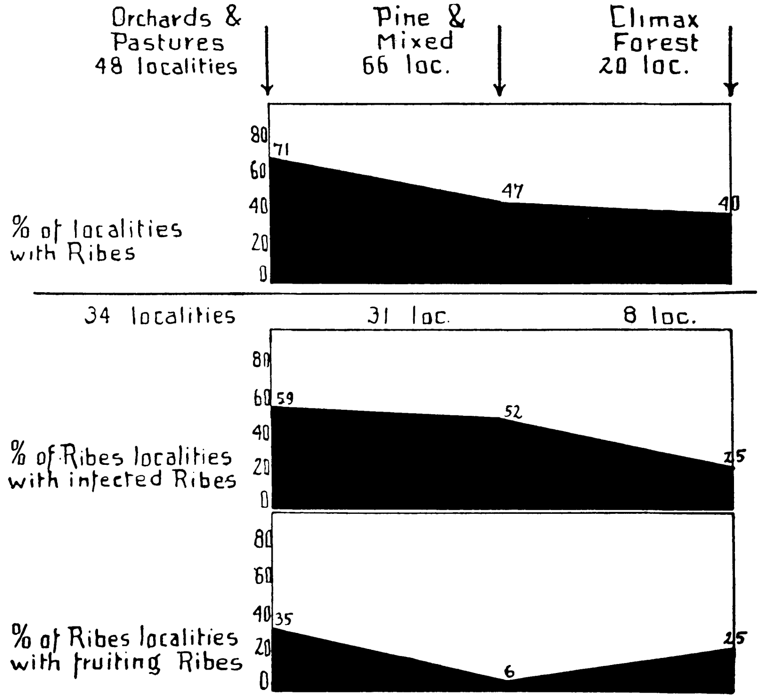

FIG. 3. Importance of Ribes in various stages of the secondary succession; relation of infection and fruiting to successional stage.

In a comparative study of leaf area as affected by environment, light being specially considered, Mr. Philip Brierley, my field assistant, discovered that in unit time (one season's growth) the gooseberries in the open pioneer stages of the succession produced an area of leaf surface 22 percent greater than those in the closed forest, the difference being due to greater average shoot length and consequent larger number of leaves, which more than balanced the smaller average size of leaf.

We conclude, therefore, that the gooseberries are abundant, large, and healthy in the early stages of the succession, fruiting heavily and also heavily infected; that they decrease in number and robustness as the succession advances, and in amount of fruit and infection as well; and that in the mature climax forest they seem near to elimination, those remaining bearing practically no fruit and almost no infection. The explanation of these facts is next in order.

b. Modes of Dissemination.—There are four possibilities: wind, gravity, running water, animals. The first may be dismissed. Gravity may carry the berries for short distances where slopes are steep and thus bring about occasional establishment in unusual situations. Running water may do likewise, and this doubtless accounts for the rather frequent occurrence of bushes along stream courses in deep forest. Both these factors are relatively unimportant beside the last. The two groups of animals that are effective disseminators are certain birds, and chipmunks and other small rodents. I have been unable to obtain sufficient data to warrant extended discussion of the latter.

The evidence as to birds is fairly satisfactory. The simplest method of approach is first of all to determine upon a list of the habitual fruit eaters, which has been done with the aid of all available literature, the result being given in Table I. The next step is to classify these twenty-six species according to habitat. Adams[2] has shown that there is a definite ecological succession of birds. Certain groups of species, or bird communities, are related to certain plant communities, and as the latter replace one another in the course of successional development, the bird communities change likewise. The bird population of the climax forest is thus very different from that which was associated with the temporary pasture stage which preceded its establishment, and which may very likely be found in some nearby locality where vegetational development has not progressed so far. Allowance must be made for the greater mobility of the bird population, resulting in less definiteness than is to be found in the plant communities. In the secondary successions of the New England region the greatest change in bird life accompanies the transition from open pasture to mixed woodland; the change from that to climax being much less significant so far as birds are concerned. For brief discussion, therefore, we may fairly contrast the birds of the open with the birds of the forest. An intermediate class must be inserted to provide for those species that are not strictly confined to either community. In the following table the general classification has been made from the literature, especially the publications of the Biological Survey. That organization has also kindly furnished the results of all stomach analyses in which evidence of *Ribes* was obtained, and these data have been added, the denominator representing the total number of analyses, the numerator the number containing *Ribes;* with the resulting percentage.

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[2] Adams, C. C., " The Ecological Succession of Birds," The Auk **25**: 109–153, 1908.

TABLE 1. *The relation of birds to the dissemination of Ribes*
Showing number of analyses containing Ribes seeds, total analyses, and resulting percentage with Ribes seeds

With Ribes Records

OPEN		UNRESTRICTED		FOREST	
Catbird, 20/677	3.00%	Wood Thrush, 1/173	.58%	Hermit Thrush, 3/639	.47%
Chewink, 10/683	1.47	Red-headed Woodpecker, 3/534	.56	Ruffed Grouse, 1/250	.43
Blue Jay, 9/678	1.32	Red-eyed Vireo, 1/654	.15	Olive-backed Thrush, 1/476	.21
Cedar Waxwing, 2/210	.95				
Robin, 13/1392	.93				
Brown Thrasher, 6/660	.91				
Bluebird, 2/859	.23				
Crow, 4/2215	.18				
Flicker, 1/718	.14				
Kingbird, 1/711	.14				

No Ribes Records

Chipping Sparrow	Rose-breasted Grosbeak	Purple Finch
Song Sparrow	Baltimore Oriole	Wilson's Thrush
Warbling Vireo	Yellow-bellied Sapsucker	
	Downy Woodpecker	
	Hairy Woodpecker	

From this table we draw the following facts: The birds of the forest, almost without exception, do not eat fruit. Of the birds of the open, many eat fruit more or less, and of the thirteen listed, ten have records of *Ribes* to their credit. Of the eight classified as unrestricted, only three have *Ribes* records.

The third step relates to the comparative abundance of the various fruit eaters. Nearly all the very abundant birds fall in the "open" column; all but two of these are exceedingly common. Only two or three, at the most, of the "unrestricted" species can fairly be classed with the majority of the first group as to abundance. The remainder of the "unrestricted" birds and the forest birds are relatively infrequent.

We conclude, therefore, that the fruit-eating birds of the open, which do not frequent the forest, are numerous in species and especially abundant in individuals; that most of them have *Ribes* records, including all the high percentages; and that as a class they are very effective as planters of *Ribes*. The birds which frequent both open country and forest are fairly numerous in species, but are nearly all relatively uncommon; few have *Ribes* records and all the percentages are low. Seeding of *Ribes* in the forest due to this class may occur, but must be of very slight importance. The same may be said of the species exclusively of the forest. The abundance of gooseberries in pastures and cleared grounds in general hardly needs further explanation. Additional evidence of incidental nature is found in the remarkably consistent occurrence of gooseberry bushes close to ancient apple trees in deserted orchards and beside isolated pasture trees; and in the occasional bushes growing high in crotches.

c. Subsequent History.—We have seen that nearly all of the seeding of gooseberries, from extraneous sources, is due to certain fruit-eating birds, and that it takes place almost entirely in the early stages of the secondary successions, while the vegetation is in the pasture, old orchard, or some other open sort of condition. The subsequent vegetational history, whatever the invading tree species, is one of increasing density and shade, and the fruit-eating birds are gradually eliminated and the insect-eating species of the forest take their place. There is thus no further opportunity for the seeding in of *Ribes* in any quantity from extraneous sources. An occasional plant may become established through the agency of some stray pasture bird, or forest bird that has found gooseberries to its taste, or through water or gravity. All these combined can not bring in *Ribes* in appreciable numbers. Practically all of the gooseberries found in closed forest (and they are sometimes rather abundant in such places) must then be either original bushes surviving from open conditions or their direct progeny. There is abundant evidence that gooseberries may be long-lived even under relatively unfavorable conditions. Their persistence in deep forest is thus not surprising. As the shade increases in the course of successional development, the *Ribes* bushes take on the characteristic forest form of single weak spindling shoots, often prostrate, instead of the sturdy clump characteristic of the open pasture. Moisture and light conditions now favor the process of layering, and the plant lives on from year to year, dying off behind and continually renewing itself by producing fresh shoots. In this way it may persist for many years, but apparently is ultimately doomed to extinction.

It has been shown that the abundance of fruiting decreases strikingly with increase of shade, so that in the climax forest it is rare to find any fruit at all. Thus the plant must fail to perpetuate itself, and given time and freedom from disturbing agencies, *Ribes* will ultimately practically disappear from the forest community.

III. Practical Applications

1. The study shows that no plant community may be consistently and safely disregarded in the search for *Ribes*. The only possibility is the beech-maple-hemlock climax, and this is so limited in extent in the region where eradication is likely to be practiced that its immunity, even if true, is of little

practical significance. The great mass of the country is either favorable for *Ribes* introduction at the present time or may support *Ribes* holding over from former conditions.

2. It seems possible to prophesy with reasonable certainty whether a given tract, once made free of *Ribes,* will remain so indefinitely, or will have to be watched carefully from year to year. In general, closed forest, once thoroughly cleaned of gooseberries, can be safely disregarded in the future, since there are no effective agencies that will renew the species from without. Any individuals that do become established will develop a minimum of infection and of fruit in such places. Open pastures, old orchards, thickets, and similar places must be carefully watched for new arrivals, since the agents of dissemination are continually active therein, and infection is likely to be heavy. Thorough care of such critical places will also operate to prevent accidental introduction of seed into nearby closed forest.